RESOURCE PARTITIONING IN CHLOROPIDAE (DIPTERA) OF A FRESHWATER MARSH

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Abstract. —Information is presented on the spatial distribution, temporal occurrence, and larval trophic habits of Chloropidae found in a northeastern Ohio freshwater marsh. Differential utilization of marsh vegetation was apparent, with the majority of species occurring in a stand of the spike-rush, *Eleocharis smallii* Britt. Within this vegetation type, chloropid species exhibited trophic partitioning by utilizing different larval foods.

The Chloropidae consist of 53 genera and some 287 species in the Nearctic Region (Sabrosky, 1987). Many chloropids are phytophagous, feeding on crop species (Cunliffe, 1925; Empson, 1957) as well as economically unimportant monocots (Wendt, 1968; Wearsch, 1968; Rogers, 1970), whereas other species are saprophagous. Valley et al. (1969) presented information concerning the larval foods of 26 Nearctic species, reporting that several species were associated with freshwater monocots such as sedges, rushes, and grasses. A recent study of a freshwater marsh in northeastern Ohio (Todd, 1985) also indicates that chloropids are well represented in stands of wetland monocots, with a particularly large array of species occurring in a plant association dominated by spike-rush, *Eleocharis smallii* Britt. This paper presents information concerning the spatial distribution, temporal occurrence, and larval food utilization of chloropid species occurring in a freshwater marsh. We then propose possible resource partitioning mechanisms affecting the Chloropidae encountered in a stand of *E. smallii.*

Materials and Methods

The freshwater marsh utilized in this study was located near Kent, Ohio, 0.8 km east of the Kent State University campus. The marsh measured approximately 4978 m² and consisted of a spatial mosaic of 8 vegetation types, most of which existed in nearly monoculture condition (Todd and Foote, 1987): (1) *Phalaris arundinacea* L. (reed canary grass), (2) *Typha-Phalaris* (equally divided between cattail and grass), (3) *Carex lacustris* Willd. (sedge), (4) *Carex stricta* Lam. (sedge), (5) *Eleocharis smallii* Britt. (spike-rush), (6) *Typha latifolia* L. (broad-leaved cattail), (7) *Nuphar lutea* Sibth. and Smith (yellow water lily), and (8) *Sparganium eurycarpum* Engelm. (bur-reed).

Eleocharis smallii formed a single stand of 70 m² in the marsh, and during spring and early summer consisted of scattered patches growing in approximately 12–15 cm of standing water. *Eleocharis* did not become a noticeable component of the marsh vegetation until mid-July, at which time the stems grew above the water surface. Once established, the patches measured 40–45 cm

Table 1.   Chloropidae collected in marsh vegetation. Vegetation types are listed in decreasing order of chloropid occurrence. PA = *Phalaris arundinacea*; TP = *Typha-Phalaris*; CL = *Carex lacustris*; CS = *Carex stricta*; ES = *Eleocharis smallii*; NL = *Nuphar lutea*; TL = *Typha latifolia*; SE = *Sparganium eurycarpum.*

Species	Vegetation Types
Apallates neocoxendix (Sabrosky)	ES, PA, CS
Chlorops certimus Adams	CL
Chlorops obscuricornis Loew	ES, CL, NL
Conioscinella sp.	CL
Diplotoxa inclinata Becker	ES
Diplotoxa nigripes (Coquillett)	ES, NL
Diplotoxa sp. nr. *nigripes*	ES
Diplotoxa sp.	ES
Elachiptera nigriceps (Loew)	ES, CL, SE
Elachiptera sp.	SE
Epichlorops exilis (Coquillett)	CL
Eribolus longulus (Loew)	CL, SE, ES, PA
Eribolus nanus (Zetterstedt)	ES, CL
Liohippelates bishoppi (Sabrosky)	NL
Oscinella frit L.	PA, CL, SE
Pseudopachychaeta approximatonervis (Zetterstedt)	ES, SE, TL, CS
Rhopalopterum atriceps (Loew)	PA
Rhopalopterum carbonarium (Loew)	CS, CL, PA, NL, TL, TP, ES, SE
Thaumatomyia bistriata (Walker)	PA
Thaumatomyia glabra (Meigen)	PA, CL, CS
Thaumatomyia grata (Loew)	SE

in height and were interspersed among areas of open water. As summer progressed, the water level dropped, and the *Eleocharis* stand existed on a highly organic mud substrate. A few individuals of *Sagittaria latifolia* Willd. (broad-leaved arrowhead) invaded *Eleocharis* in early August, and a noticeable algal flora usually was present on the mud substrate. Decaying plant material accumulated throughout the summer.

For collecting purposes, a 5.0 × 10.0 m quadrat was established within each vegetation type. Sampling for adult chloropids was conducted between June and October, 1984, using a simplified version of the pan trap described by Grigarick (1959). A 38.5 × 14.0 × 4.5 cm yellow plastic container was filled with a detergent-water solution to a depth of approximately 2.0 cm. Disney et al. (1982) found yellow to be most effective in collecting Diptera from grass-like areas. One pan was placed in the center of each quadrat biweekly and left in place for 24 h.

Trapped insects were removed and stored in 70% ethyl alcohol. Additional specimens were obtained by sweeping vegetation with a standard 30.5 cm aerial insect net. Sweeping was conducted biweekly before placement of the pan traps and consisted of 10 back and forth sweeps along the 10 m center line of a quadrat. All sampling was done in the early afternoon hours.

Material obtained from the sweeps and pan traps was combined to compile species lists for each vegetation type. Relative abundance and percent presence values were calculated for all species collected from each vegetation type. Relative abundance values were further categorized according to a method developed by Scheiring and Foote (1973) and are defined as follows: 1–2% rare (r); 3–8% occasional (occ); 9–14% common (c); 15–25% abundant (a); and 26–100% very abundant (va).

To quantify utilization of spatial and temporal resources, niche breadth and overlap
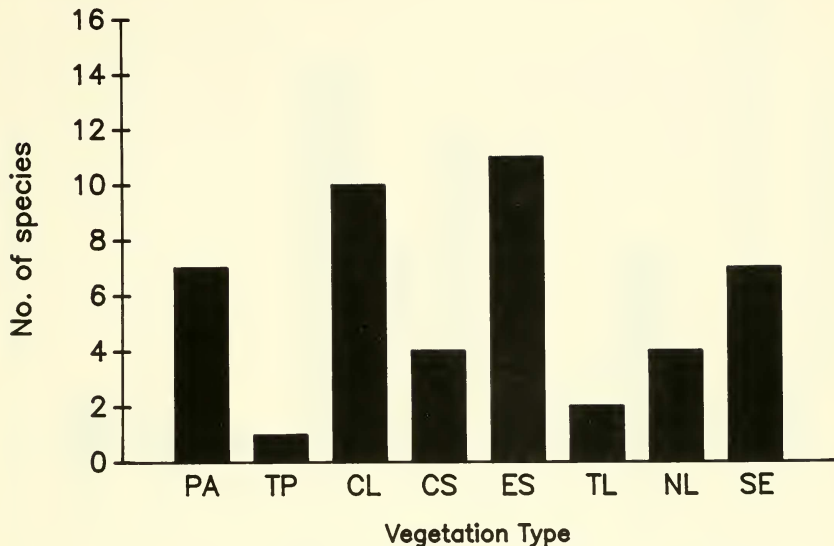
Fig. 1. Number of species of Chloropidae collected in 8 vegetation types of the freshwater marsh. PA = *P. arundinacea*, TP = *Typha-Phalaris*, CL = *C. lacustris*, CS = *C. stricta*, ES = *E. smallii*, TL = *T. latifolia*, NL = *N. lutea*, SE = *S. eurycarpum*.

values (Colwell and Futuyma, 1971) were calculated for all chloropids determined to species. Breadth values ranged from 0.00 to 1.00. The minimum value (0.00) indicates extreme specialization, and the maximum value (1.00) indicates generalization. Overlap values also ranged from 0.00 to 1.00. The minimum value (0.00) was obtained when two species shared no resource in common, whereas the maximum value (1.00) was obtained when the proportional distribution of two species among a resource was the same. Information on larval feeding habits was taken from the literature.

RESULTS

A total of 225 chloropids of 21 species and 12 genera was collected from the 8 quadrats established within the marsh (Table 1). Chloropid species and individuals were most commonly collected in *E. smallii, C. lacustris,* and *P. arundinacea* (Figs. 1,

2). Temporal data indicate that species richness was highest in the marsh between mid-July and mid-August (Fig. 3). A secondary peak was observed in early June, followed by a period in which no species were collected again until early July. From late August until the completion of the study, species richness remained low ($\bar{x} = 3$) but fairly constant. The majority of chloropid individuals ($>70\%$) was also collected between mid-July and mid-August (Fig. 4).

Field collections indicate that the stand of *E. smallii* contained 44% of all chloropid species and 23% of all chloropid individuals taken during the study (Figs. 1, 2). Ninety-nine individuals were collected, comprising 7 genera and 11 species (Table 2). Relative abundance values indicate that 4 species can be considered very abundant (va), abundant (a) or common (c) in *Eleocharis*: *Apallates neocoxendix* (Sabrosky) (c), *Chlorops obscuricornis* Loew (va), *Diplotoxa inclinata*
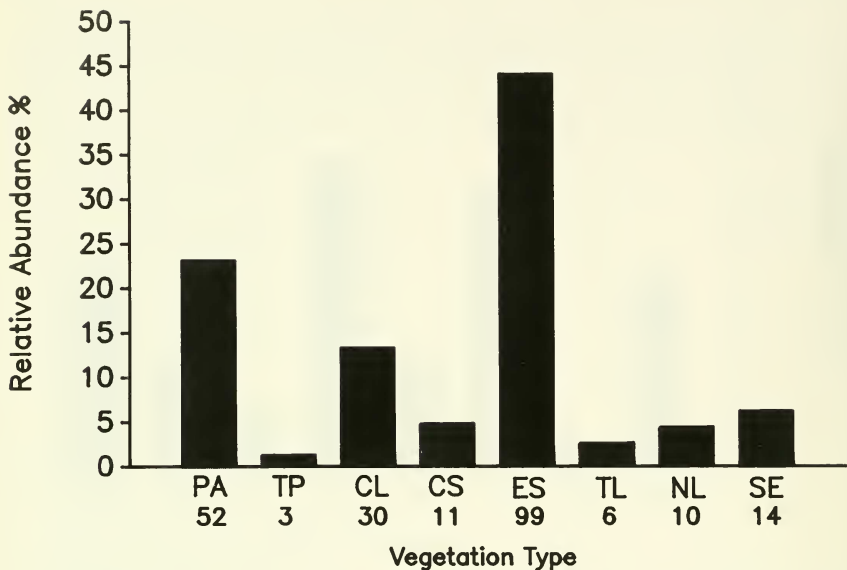
Fig. 2.   Relative abundance of species of chloropidae collected in 8 vegetation types of the freshwater marsh. PA = *P. arundinacea,* TP = *Typha-Phalaris,* CL = *C. lacustris,* CS = *C. stricta,* ES = *E. smallii,* TL = *T. latifolia,* NL = *N. lutea,* SE = *S. eurycarpum.* Actual number of specimens collected in each vegetation type is given below the x-axis.

Becker (c), and *Diplotoxa nigripes* (Coquillett) (a). These and other species are discussed below.

Apallates neocoxendix was collected only between early and mid-August (Table 2), and its percent presence (Table 2) and temporal breadth values (Table 3) were low. This species was most similar in temporal occurrence to *C. obscuricornis* (Table 3). Little information has been published concerning the trophic habits of *A. neocoxendix,* although larvae probably feed on decaying plant material (Starks and Thurston, 1962; Wheeler, 1973).

Chlorops obscuricornis was collected from early August to late September, with peak emergence in mid-August (Table 2). This species exhibited a moderately high temporal breadth value, and was most similar in temporal occurrence to *A. neocoxendix*

(Table 3). Larvae of this species feed as primary invaders of *Eleocharis* stems (Valley et al., 1969).

Diplotoxa inclinata was collected only between early and mid-August (Table 2), and was most similar in temporal occurrence to *Elachiptera nigriceps* (Table 3). Larvae attack rhizomes of *Eleocharis* (Wearsch, 1968). Females deposit eggs on stems just above the water surface, and newly hatched larvae penetrate the stem and do some feeding before moving to the rhizomes to complete development.

Diplotoxa nigripes was collected between early August and mid-October (Table 2), with the majority of individuals occurring in late September. Wearsch (1968) collected numerous adults of this species from mid-June through early October in stands of *E. smallii.* Therefore, the temporal breadth
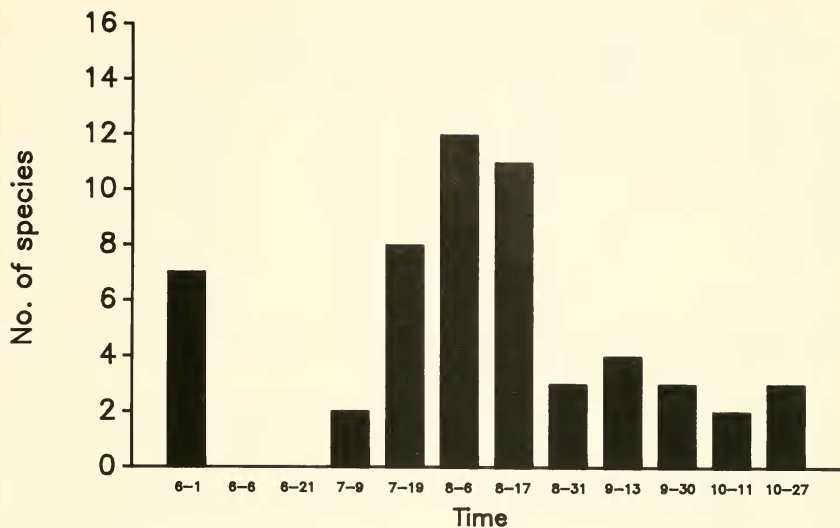
Fig. 3.   Number of species of Chloropidae occurring at 12 time intervals in the freshwater marsh.
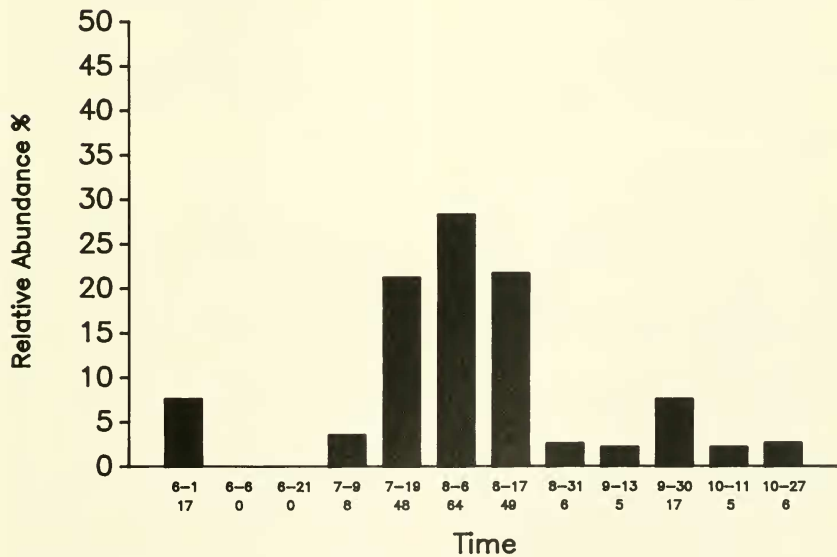

Fig. 4.   Relative abundance of species of Chloropidae occurring at 12 time intervals in the freshwater marsh. Actual number of specimens collected on each date is given below the x-axis.

Table 2. Abundance data, flight periods and larval foods of Chloropidae collected in *E. smallii*.

Species	Number Collected	Relative Abundance	Percent Presence	Flight Period	Larval Food
A. neocoxendix	10	10.10	16.67	Aug.	Decaying vegetation
C. obscuricornis	44	44.44	33.33	Aug.–Sept.	*Eleocharis* stems
D. inclinata	12	12.12	8.33	Aug.	*Eleocharis* rhizomes
D. nigripes	15	15.15	33.33	Aug.–Oct.	*Eleocharis* stems
D. sp. nr. *nigripes*	2	2.02	8.33	Aug.	Unknown
Diplotoxa sp.	2	2.02	16.67	Aug.	Unknown
E. nigriceps	4	4.04	25.00	Aug.	Decaying vegetation
E. longulus	3	3.03	8.33	Oct.	Damaged monocot stems
E. nanus	2	2.02	8.33	Oct.	Damaged monocot stems
P. approximatonervis	3	3.03	8.33	Aug.	*Eleocharis* seeds
R. carbonarium	2	2.02	16.67	Aug.	Damaged monocot stems

value attained for *D. nigripes* in the present study (0.47) (Table 3) probably would have been considerably higher had this vegetation existed in the marsh in June. *Diplotoxa nigripes* was most similar in temporal occurrence to *C. obscuricornis* (Table 3). Larvae of *D. nigripes* feed as primary invaders of *Eleocharis* stems (Valley et al., 1969).

Elachiptera nigriceps was collected between early and late August (Table 2), and was most similar in temporal occurrence to *D. inclinata* (Table 3). Larvae of *E. nigriceps* feed on decaying vegetation (Valley et al., 1969).

Eribolus longulus was collected only in early October (Table 2), and thus exhibited extreme temporal specialization (0.00) (Table 3). This species was most similar in temporal occurrence to *D. nigripes* (Table 3). Larvae feed as secondary invaders of a variety of wetland monocots (Valley et al., 1969), although we did not encounter larvae in stems of *Eleocharis*.

Eribolus nanus was collected in late October (Table 2), and exhibited extreme temporal specialization (0.00) (Table 3). The flight period of this species did not overlap with that of any other chloropid collected in *Eleocharis* (Table 3). Larvae of *E. nanus* feed as secondary invaders of various wetland monocots (Valley et al., 1969).

Pseudopachychaeta approximatonervis was collected in mid-August (Table 2), and was most similar in temporal occurrence to *A. neocoxendix* (Table 3). Larvae are seed predators in *Eleocharis* inflorescences (Valley et al., 1969).

Rhopalopterum carbonarium was collected from mid- to late August (Table 2), and was most similar in temporal occurrence to *C. obscuricornis* (Table 3). Larvae are known to be secondary invaders of damaged stems of herbaceous wetland plants (Valley et al., 1969). We did not encounter larvae in stems of *Eleocharis*.

DISCUSSION

Prior to the 1970's, most of the research on insects in wetlands focused on taxonomic composition or the biology of selected species (Judd, 1949; Davis and Gray, 1966). More recently, research has concentrated on determining the mechanisms affecting insect community organization (Tschirnhaus, 1981; Price, 1983). Several authors have suggested that resource partitioning operates to segregate similar species that could be potential competitors for a limited resource. Partitioning may involve utilization of different plant species (Blair and Foote, 1984) or plant parts (Root and Chaplin, 1976), microhabitat distribution (Hicks and

Table 3. Temporal niche breadth ( ) and overlap values for 9 chloropid species collected in *E. smallii.*

Species	1	2	3	4	5	6	7	8	9
1. *A. neocoxendix* (.29)	—	0.84	0.65	0.13	0.65	0.00	0.00	0.60	0.50
2. *C. obscuricornis* (.47)		—	0.52	0.27	0.61	0.00	0.00	0.57	0.59
3. *D. inclinata* (.24)			—	0.13	0.75	0.00	0.00	0.25	0.25
4. *D. nigripes* (.47)				—	0.20	0.13	0.00	0.07	0.13
5. *E. nigriceps* (.45)					—	0.00	0.00	0.25	0.50
6. *E. longulus* (.00)						—	0.00	0.00	0.00
7. *E. nanus* (.00)							—	0.00	0.00
8. *P. approximatonervis* (.00)								—	0.50
9. *R. carbonarium* (.30)									—

Tahvanainen, 1974), or temporal occurrence (Thornhill, 1980; Stave and Shiff, 1981).

The results of this study indicate that resource partitioning does occur among the Chloropidae inhabiting the marsh. This is revealed by examining the spatial distribution, temporal occurrence, and larval trophic habits of the component species (Tables 1, 2). In agreement with previous studies (Schoener, 1974), the spatial resource axis (vegetation type) is of primary importance in segregating species, followed by the trophic and temporal axes, respectively. For example, collection data indicate that *A. neocoxendix, C. obscuricornis, D. nigripes, D. inclinata,* and *P. approximatonervis* were largely or exclusively collected from *E. smallii,* whereas *Oscinella frit* and *Thaumatomyia glabra* were collected most abundantly in *P. arundinacea* (Table 1). Because the majority of chloropid species (11) and individuals (99) was collected from *E. smallii,* this discussion focuses on possible partitioning mechanisms among its component species. Several authors have suggested that competition may not be important in dictating the niches of phytophagous insects (Strong et al., 1984). Similarly, we have no evidence that resources were limiting or that competition was operating to structure chloropid community organization in the marsh.

Trophic habits appear to be important in

segregating at least 5 of the species occurring in *Eleocharis* (Table 2). Larvae of *A. neocoxendix* feed on decaying vegetation, a trophic resource which was utilized by only one other chloropid species, *Elachiptera nigriceps.* Larvae of *D. inclinata* feed in the rhizomes of *Eleocharis,* and are thereby trophically isolated from other species. In contrast, *C. obscuricornis* and *D. nigripes* are both primary invaders of *Eleocharis* stems. However, they differ in their peak emergence times (Table 2). *Chlorops obscuricornis* is abundant much earlier in the season than is *D. nigripes,* and temporal segregation appears to be important in preventing potential competition between larvae of these species should their populations attain levels that could result in *Eleocharis* stems becoming a limiting resource. Three species, *E. longulus, E. nanus,* and *R. carbonarium* are known to be secondary invaders of wetland monocots damaged by other insect species. Adult numbers in the *Eleocharis* stand were relatively low, and it is probable that the larvae do not utilize this particular plant species. Finally, *P. approximatonervis* is in a unique trophic niche in that its larvae are seed predators within *Eleocharis* inflorescences.

In summary, data indicate that the Chloropidae of a northeastern Ohio freshwater marsh exhibit resource partitioning along the spatial resource axis by differential utilization of available vegetation types. The

majority of species and individuals was ob-
tained from the spike-rush, *E. smallii.*
Within this vegetation type, chloropid
species primarily exhibited trophic parti-
tioning by utilizing different plant parts as
larval food (seeds, stem, rhizomes, decaying
tissue). Temporal partitioning was of minor
importance in segregating species, with the
flight period of most species being between
early and mid-August.

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